ONTOGENY OF THE SPORANGIA IN XIPHOPTERIS SERRULATA AND PYRROSIA NUDA [1]

KENNETH A. WILSON

IN SPITE OF ALL the recent discussion of relationships and classification of such well-known genera as *Vittaria* and *Polypodium*, and such of their presumed allies as *Dipteris*, *Cheiropleuria*, and *Platycerium*, no attempts appear to have been made to correlate the details of sporangial structure with cytological and other morphological evidence (e.g., the nature of the gametophytes) which has recently been accumulating. It is surprising that, in view of the emphasis which is placed on the reproductive parts of flowering plants, the sporangial structure has for so long escaped detailed investigation. Undoubtedly one of the main factors in causing this delay in their study is the opinion that the sporangia of the "higher" or polypodiaceous ferns are so simple that they do not by themselves give adequate evidence of relationship (Holttum, 1954). It is true that these minute sporangia are deceptively similar in appearance. However, before one can determine accurately whether sporangial structures are comparable it is important to know the precise details of leptosporangial ontogeny. Ontogenetic knowledge should lead to (1) clearer concepts of homology between parts of sporangia of different species, and (2) demonstrations that some apparent homologies do not exist. Only then can the details of the mature sporangium be clearly understood, and only then can there be a basis for the interpretation of presumably homologous parts of a large number of mature sporangia.

In an earlier paper (Wilson, 1958), the ontogenetic steps in the formation of the mature sporangium of *Phlebodium aureum* (L.) J. Sm. (Polypodiaceae sensu strictu) were presented. It was shown that the sporangial stalk results from cells intercalated in the first segments of the sporangial primordium rather than by the activity of an apical cell as has been generally believed. Furthermore, it was found that the stalk of the sporangium and the jacket of the capsule are produced by the subdivision of 5 initials or "segments." Segment 0 contributes only to the formation of the stalk, segment I to a portion of the stalk and part of the proximal face of the capsule, segment II to the stomial region, the stalk, and to the proximal and distal faces of the capsule, and segments III and IV to the rest of the annulus and to both the proximal and distal faces of the capsule.

However, the study of sporangial ontogeny in *Phlebodium* still left several questions unanswered. *Phlebodium* has a two-rowed stalk; how is a one-rowed stalk produced? Do the sporangia of another genus in the same family develop in the same manner? What difference, if any,

[1] A portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.

would be found in the ontogeny of the sporangia in a species of a different family?

In an attempt to answer these questions two fern species were chosen for study: *Xiphopteris serrulata* (Sw.) Kaulf. (Grammitidaceae) and *Pyrrosia nuda* (Gies.) Ching (Polypodiaceae). In the present paper, the developmental sequence in the formation of the sporangia in the two species is described and a comparison is made with the ontogeny of the sporangia in *Phlebodium aureum*.

ACKNOWLEDGMENTS

I am particularly indebted to Dr. Warren H. Wagner, Jr. for his patient and helpful directions and criticisms during the entire course of this investigation. The material of *Xiphopteris serrulata* used in this study was collected by me during an expedition to Jamaica, The West Indies. I am deeply grateful to Dr. Grady L. Webster and to Professor H. H. Bartlett for making this field study possible.

MATERIAL AND METHODS

The plant material of *Xiphopteris serrulata* was collected in Portland Parish, Jamaica, in 1954 (*K. A. Wilson & W. Murray 588*). *Pyrrosia nuda* is growing at the Botanical Gardens of the University of Michigan, and the material was collected there (UMBG *19980*; from Assam, India, *W. Koelz 11716A*). Specimens of both species have been deposited in the Herbarium of the University of Michigan, and duplicates of *Xiphopteris serrulata* have been distributed to several other herbaria.

Young sori which had been preserved in F.A.A. were selected, embedded in paraffin, and sectioned. *Xiphopteris* was sectioned at 12 microns, while *Pyrrosia*, because of the larger size of the young sporangia, was sectioned at 15 microns. The sections were stained in Conant's quadruple stain (Johansen, 1940). Sori in various stages of development were also cleared by the sodium hydroxide technique (Foster, 1949) and then stained in 3 per cent tannic acid in 50 per cent alcohol and 3 per cent ferric chloride in 50 per cent alcohol. After dehydration in alcohol, the sporangia were teased out and mounted in Diaphane. Because of the thickness of the frond of *Pyrrosia* and the deeply sunken sori, the above method, which was successful for *Xiphopteris*, proved to be of value only for the sporangia in the later stages of development. In order to study the earlier stages, 75-micron sections of fixed *Pyrrosia* material were cut on the freezing microtome. These sections were cleared and stained as outlined above and then mounted in Diaphane without further dissection. When bleaching was necessary, a 50 per cent aqueous solution of Clorox was used. The mature sporangia were studied in water mounts since dehydration led to the dehiscence of the capsule. All illustrations were made with the aid of a camera lucida.

MORPHOLOGICAL OBSERVATIONS

1. Xiphopteris serrulata

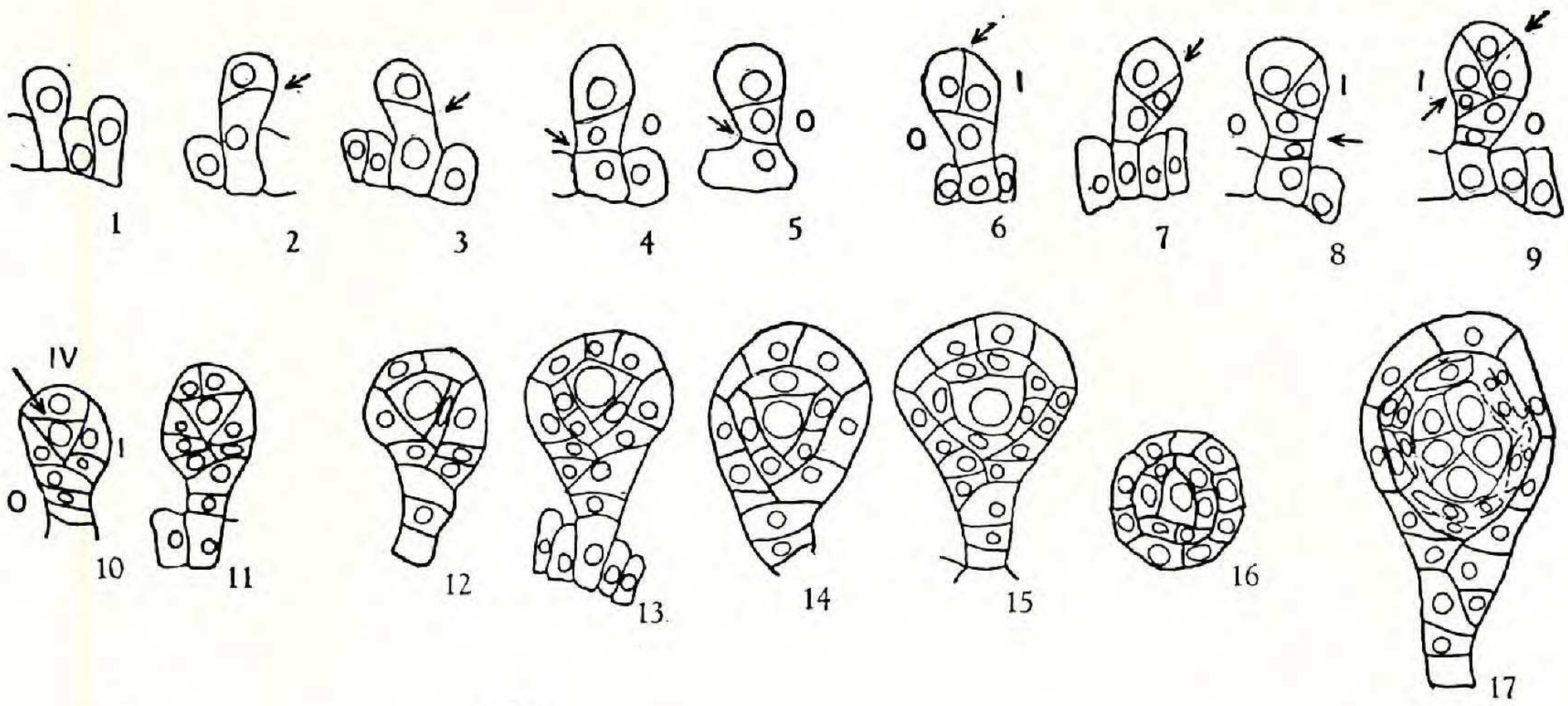
The swollen sporangial initial of *Xiphopteris serrulata* is first divided by a cell-wall which is slightly inclined but which never reaches the level of the receptacular cells (*figs. 2, 3*). This division is soon followed by the formation of a second wall which is transverse and intercalated in the lower cell of the initial (*figs. 4, 5*). This wall is produced on a level with the surface of the adjacent receptacular cells, and separates the sporangial primordium from a basal cell. The basal cell undergoes no further division and takes no part in the subsequent development of the sporangium. The sporangial initial at this stage consists of two cells: a proximal cell, segment 0, and a distal cell, the mother initial.

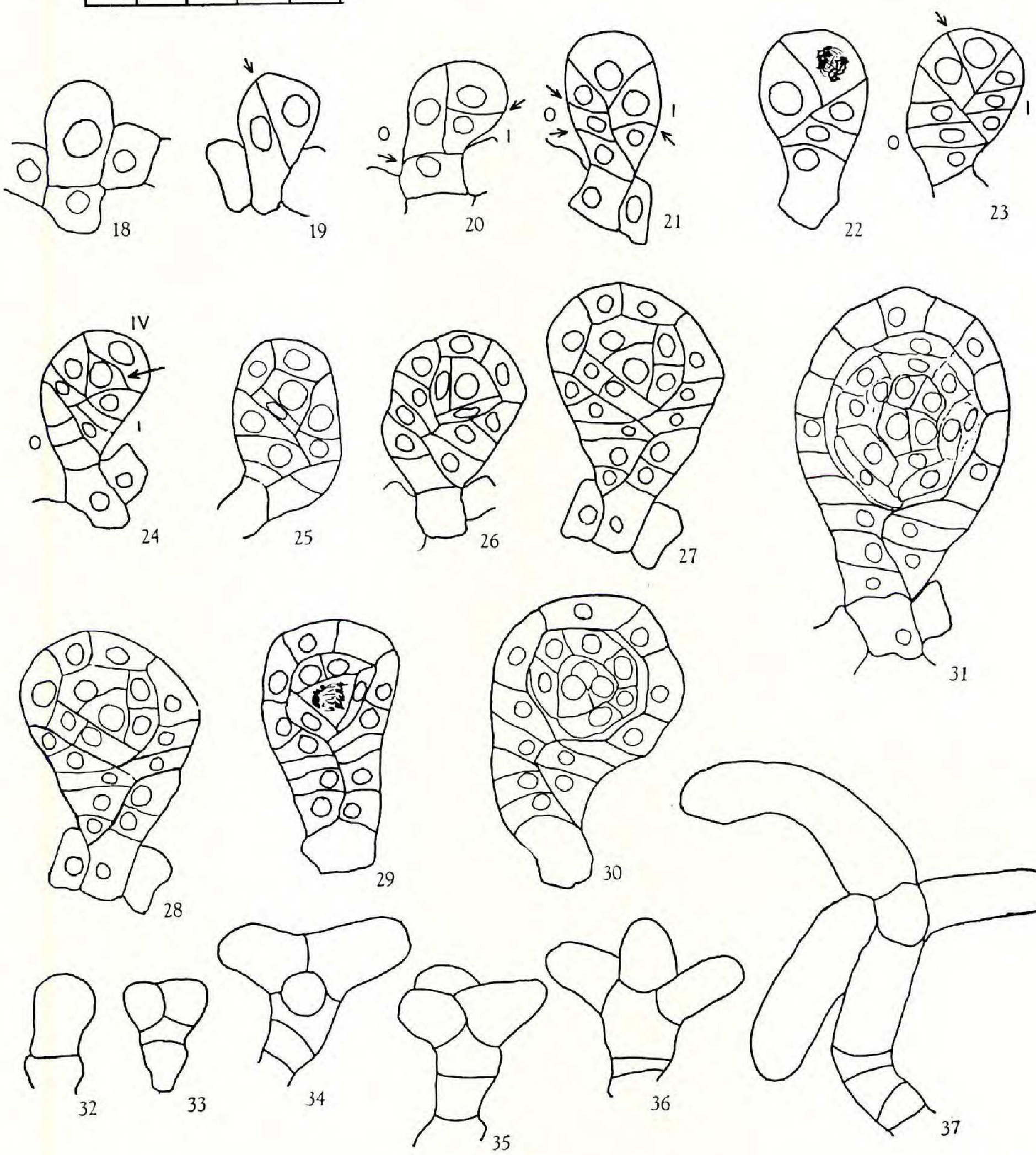
The mother initial divides and cuts off, by a series of three oblique walls, segments I, II and III, which contribute to the jacket layer of the capsule and the distal, three-rowed portion of the stalk (*figs. 6–9*). In the meantime, horizontal intercalary divisions take place in segment 0 (*figs. 8, 9*). After the formation of segments I, II, and III, the mother initial, now shaped like an inverted three-sided pyramid, divides horizontally and produces a transverse wall which cuts off segment IV and thereby becomes completely enclosed by its daughter cells (*fig. 10*).

The enclosed tetrahedral mother initial divides in the same manner and in the same order as it did in producing segments I, II, III, and IV, so that it becomes enclosed by four cells, the tapetal initials, which separate it from the cells of the sporangial wall (*figs. 12–14*). Each of the tapetal initials becomes partitioned into four cells by means of a vertical and a horizontal anticlinal wall (*figs. 13–16*), and all sixteen cells produced by these divisions then divide periclinally to form a two-layered tapetum, which soon disorganizes, surrounding the inner sporogenous cells (*fig. 17*).

After the mother initial divides to produce the four tapetal initials, the activity of the central cell changes and it divides equally to form the sporocytes (*fig. 17*).

FIGS. 1–37. SPORANGIAL ONTOGENY IN *Xiphopteris serrulata* AND *Pyrrosia nuda*: INTERNAL SEGMENTATION. FIGS. 1–17, *Xiphopteris serrulata*: 1, Protruding initial; 2, 3, Formation of first wall; 4, 5, Formation of segment 0; 6, 7, Formation of segment I; 8, Intercalary division in segment 0; 9, Formation of segment II or segment III, intercalary division in segment I; 10, Formation of segment IV; 11, Intercalary division in segment IV; 12–15, Formation of tapetal initials; 16, Cross section of primordial capsule; 17, Formation of sporocytes. FIGS. 18–37, *Pyrrosia nuda*: 18, Protruding initial; 19, Formation of first wall; 20, Formation of segments 0 and I; 21, Intercalary divisions in segments 0 and I; 22, 23, Formation of segment II or segment III; 24, Formation of segment IV; 25–28, Formation of tapetal initials; 29–31, Formation of sporocytes; 32–37, Various stages in the ontogeny of the paraphyses. Arrows point to newly formed walls. Roman numerals identify sporangial segments.





FIGS 1–37. SPORANGIAL ONTOGENY IN *Xiphopteris serrulata* AND *Pyrrosia nuda*.

All divisions that take place in segment 0 are horizontal; there are never any vertical walls formed in the segment. As a result of the position and inclination of the first wall formed in the sporangial initial, segment I never reaches the level of the cells of the receptacle. Therefore, since only segment 0 contributes to the base of the sporangial stalk, and since the divisions within this segment are only transverse, the stalk of the mature sporangium consists of a single row of cells at its base (*figs. 59–61*). On the other hand, the upper portion of the stalk beneath the capsule is three-rowed. The cells in the lower portion of segments I, II, and III each contribute to the formation of one of the three rows of cells which subtend the capsule.

While the tapetal initials and sporogenous cells are dividing, the jacket initials are becoming partitioned anticlinally to produce the exterior layer of the capsule. The first two divisions in segment I are transverse (*figs. 41–45*), and these are followed by the formation of still another cross wall in the distal portion of the segment so that segment I becomes composed of a linear series of four cells (*figs. 46, 47*).

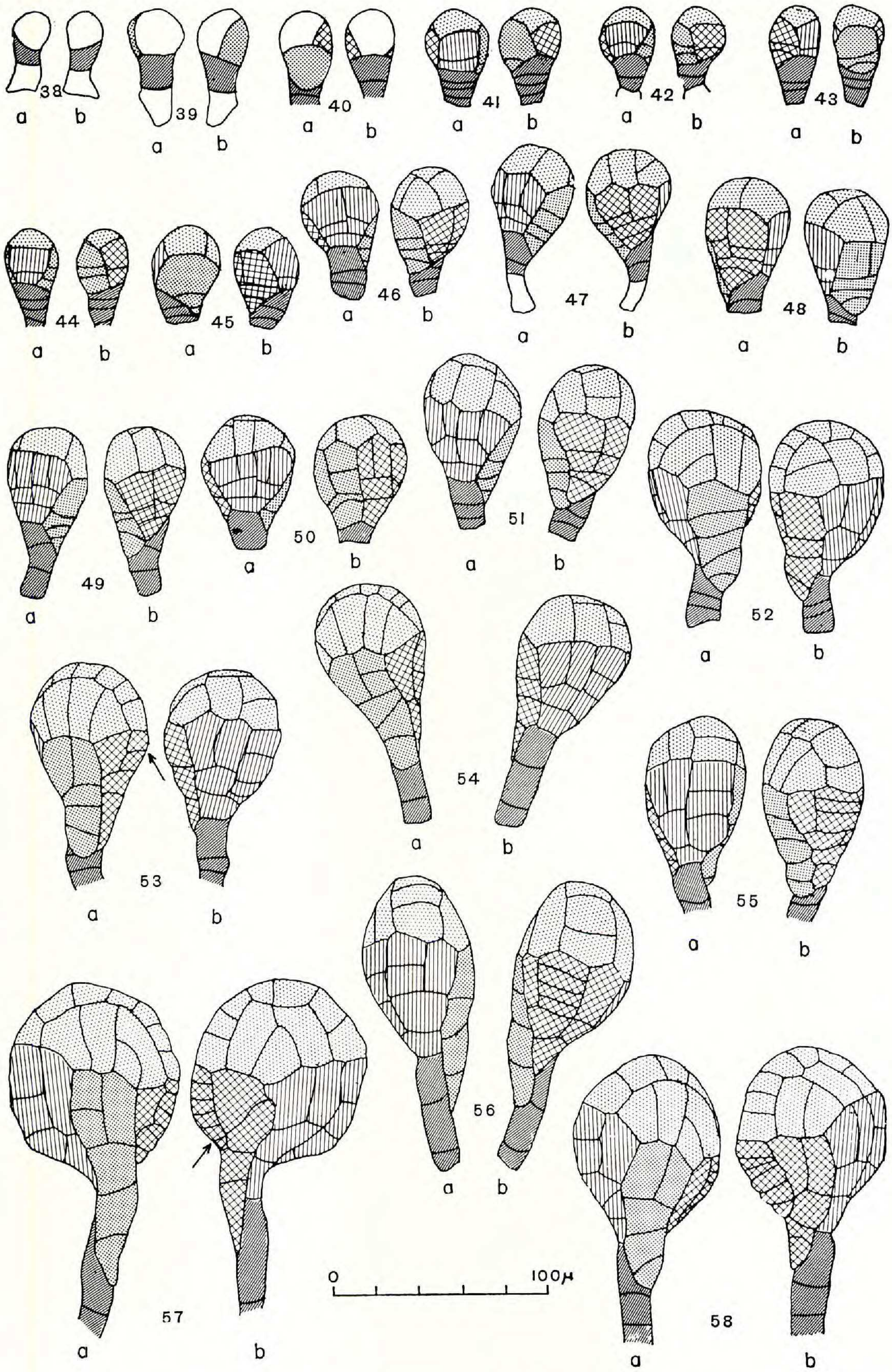
Both segment II and segment III become similarly partitioned by cross walls; however, segment II is divided by two transverse walls, while segment III becomes partitioned by only one such wall (*figs. 42, 43a*).

The cleavages in the first three capsular segments are accompanied, or soon followed, by a division in the cap cell, segment IV, which produces a wall, difficult to see in whole cleared sporangia, that extends from segment II to segment III (*fig. 45a*; *figs. 62, 63*, wall *v*). Following the first division of segment IV into two cells, each one of the cells undergoes a division by a wall perpendicular to the first one (*fig. 46b*; *figs. 62, 63*, walls *h*).

The uppermost of the four cells of segment I divides, by the formation of a vertical wall, into two cells of approximately the same size (*fig. 48b*; *fig. 63*, wall *v*). This vertical division is at times followed by a horizontal division in one of the two cells (*figs. 54a, 57a*); more frequently, however, these cells remain undivided (*figs. 53a, 58a*). The distal cells of segment I are immediately recognizable in mature sporangia and may be seen to form a portion of the capsular jacket on one side, the proximal face, of the sporangium (*figs. 59, 61*). The three cells below them, on the other hand, produce one of the three rows of cells at the base of the capsule.

The division pattern of the other capsular segments is more complex and may be understood more easily by considering the sequence of division in each of the segments separately. As the developing sporangium continues to enlarge, the uppermost of the three cells of segment II becomes divided by a vertical wall (*fig. 45b*; *fig. 63*, wall *v*), and each of the cells thereby produced now divides by forming a horizontal wall (*fig. 48a; fig. 63*, walls *h*). The cells next to segment III do not become further divided, and they can be recognized in the mature sporangia as forming part of one of the lateral walls of the capsule (*fig. 60*). These first divisions in segment II are essentially identical to those of segment I, and, as will be shown later, a similar division sequence occurs in segment III.

Additional divisions in segment II all contribute to the formation of the



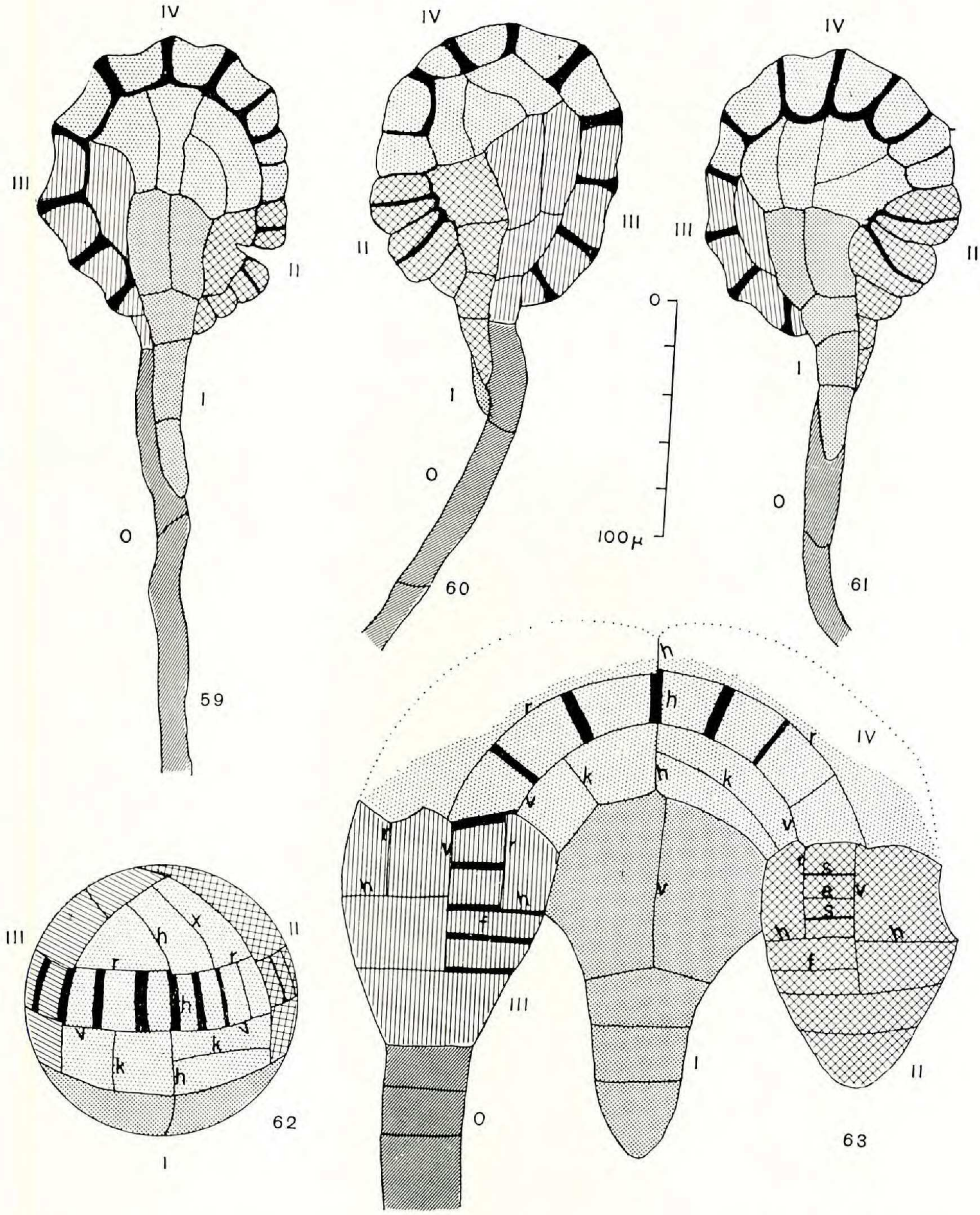
FIGS. 38–58. SPORANGIAL ONTOGENY IN *Xiphopteris serrulata*: SUPERFICIAL SEGMENTATION. Both sides of each sporangial primordium are illustrated and are designated by the letters "a" and "b." For explanation of shading see FIGS. 64–78.

stomium and its associated cells. The cell which undergoes the first division is directly related to the position of segment II with respect to segment I. It is always the uppermost cell contiguous to segment I which becomes partitioned by a vertical wall. It must be pointed out here that, in contrast to *Phlebodium aureum*, segment II is very rarely produced on the left side of segment I; in the great majority of sporangia segment II will be found to be lying to the right of segment I.

The distal cell of segment II which is contiguous to segment I becomes partitioned by a vertical wall (not shown in its first appearance; see wall *r*, *fig. 63*). The uppermost daughter cell which borders on segment I undergoes no further divisions and contributes to the formation of part of a lateral wall. However, the other daughter cell becomes partitioned by the intercalation of a horizontal wall (shown by arrow, *fig. 53a*; *fig. 63*, wall *e*). An additional horizontal wall partitions each one of these last-formed cells and produces the stomial cells (*fig. 56b*; *fig. 63*, walls *s*). As a rule the distal cell next to segment III remains undivided; however, on occasion it may become partitioned by a vertical wall (*fig. 58b*). Before the formation of the stomium, a horizontal wall is usually intercalated in the cell directly beneath the one which is divided by the vertical wall (i.e., the distal cell contiguous to segment I; shown by arrow, *fig. 57b*; *fig. 63*, wall *f*). Following the divisions which produce the stomium, no additional cleavages occur in segment II. The two lowermost cells of segment II form part of the three-rowed stalk at the base of the capsule (*fig. 60*).

Occasional failure of wall formation in segment II may lead to the formation of unusually large cells in the stomial region, as may be seen in *figure 61*. This condition is a result of the absence of the vertical wall which delimits the annular cells in segment II. A similar situation has been observed in segment III, which would result in the formation of large bow cells (*fig. 55a*).

As was stated above, the distal cell of segment III becomes dissected first by a vertical wall (*fig. 63*, wall *v*) and then by two horizontal walls (*fig. 63*, walls *h*) in much the same manner as segment II. The next divisions mirror those of segment II except for the formation of an additional wall. Both of the distal cells become divided by the formation of a vertical wall (*figs. 50a, 51a*; *fig. 63*, walls *r*), after which the cell adjacent to the one which borders on segment I is partitioned by a horizontal wall (*fig. 56a*). One wall forms in the cell below (see wall *f*, *fig. 63*), and with the production of this series of cells the subdivision of segment III is completed. As the sporangium enlarges and matures, the walls of the smaller cells in segment III, which are aligned in a vertical series, become thickened to form the cells of the bow, while the lowermost cell of this segment contributes to the formation of the three-rowed stalk (*fig. 59*). The cells between the bow cells and the cells of segment II do not become further subdivided after the division of the distal cell by the vertical wall. These cells all contribute to the formation of part of the lateral face (*fig. 60*), while the cell on the opposite side of the annular ring and in contact with segment I contributes to the other side of the capsular face (*fig. 59*).



FIGS. 59–63. MATURE SPORANGIUM OF *Xiphopteris serrulata*. 59, Proximal face; 60, Distal face; 61, Proximal face: segment II with abnormally large stomial region; 62, 63, Diagrammatic analysis of segment derivatives in the mature sporangium; 62, Top view: segment IV (adapted from Kündig); 63, segments I, II, III (adapted from Müller). Roman numerals identify sporangial segments. For explanation see text.

The first divisions of segment IV into four cells are followed by a division of the two cells contiguous to segments II and III, which produces in each cell a wall that is parallel to the first-formed wall. In other words, these walls are intercalated in the sector of segment IV on that side of the first-formed wall which is away from segment I (see walls *r*, *fig. 63*). This division sets the boundaries for the formation of the annular cells in the cap segment. A series of walls perpendicular to the first-formed wall and to the wall parallel to it produces a series of cells which differentiate into the top of the annulus. The greatest variation in the division pattern of *Xiphopteris serrulata* is seen in the partitioning of segment IV. Generally this segment contributes seven cells to the annulus; however, it may at times be observed that only six cells are produced in this series (*fig. 60*). The portion of segment IV which contributes to the proximal face of the sporangium usually becomes divided by walls formed in different planes: one wall is formed vertically while the other is variously inclined (*figs. 59, 61*; walls *k*, *figs. 62, 63*). The placement of the last cell wall in the sector of segment IV in the distal face of the sporangium also varies (wall *x*, *fig. 62*; *figs. 52b, 57b*).

2. Pyrrosia nuda

One of the most striking differences in the young sporangia of *Pyrrosia nuda* from those of *Xiphopteris*, as well as from those of *Phlebodium*, is in their size. The sporangial initials are themselves almost twice as large as those of *Phlebodium*, and well over twice the size of those of *Xiphopteris* (*fig. 18*). However, in spite of the size of the sporangial initial, the first two divisions are the same as those of *Phlebodium*. The first wall formed is oblique and extends to the level of the receptacular cells or below it (*fig. 19*). The second wall is horizontal and in line with the surface of the cells of the receptacle (*fig. 20*).

There seems to be some variation in the orientation of the wall which produces segment I. It may be noted that at times this wall is formed in such a way that it does not bisect the wall of segment 0, as it does in *Phlebodium*, but rather is so oriented that segment I fails to include the entire basal portion of the initial which is not occupied by segment 0. Consequently, the lower portion of the mother initial reaches the base of the primordium (*fig. 65*). In such circumstances, when segment II is formed it will extend to the very base of the sporangial primordium (*figs. 67a, 70a*)! This is a rare occurrence. Usually the divisions are as in *Phlebodium* and the base of the primordium is occupied by segment 0 and segment I only (*fig. 69*), resulting in a two-rowed stalk. When, however, the wall of segment I is so placed that segment II reaches the base of the sporangium, the entire stalk of the mature sporangium will be three-rowed. Although such stalks are rare, they have been observed in mature sporangia of *Pyrrosia*.

The details of the further development of the sporangium do not vary from those of either *Xiphopteris* or *Phlebodium*. Of some significance may

be the fact that a larger number of cells form the bow in *Pyrrosia* than in either of the other two genera (segment IV contributes twelve cells to the annulus), but they are formed in the same manner as has been described for *Xiphopteris* (see *figs. 18–31, 64–84*).

Stellate paraphyses occur intermixed with the sporangia of *Pyrrosia* (*fig. 85*). These arise from superficial cells of the receptacle which become divided by a transverse wall (*fig. 32*). Following the initial transverse divisions, the terminal cell of the developing paraphysis becomes bisected by a vertical wall (*fig. 33*). These two terminal cells continue to elongate, and soon, as a result of a protrusion and expansion of the cell wall beneath them, a third cell is initiated (*fig. 34*). Elongation of these cells apparently does not take place at the same rate; the newly formed cells appear to elongate more rapidly. This process is repeated many times (see *fig. 37*) and gives rise to the many-celled paraphyses. Vertical divisions in the stalk may be seen to accompany the formation of the elongated cells. On the other hand, no walls are formed in the terminal cells of the paraphysis. The elongation of the terminal cells ceases soon after the walls at their bases become thickened.

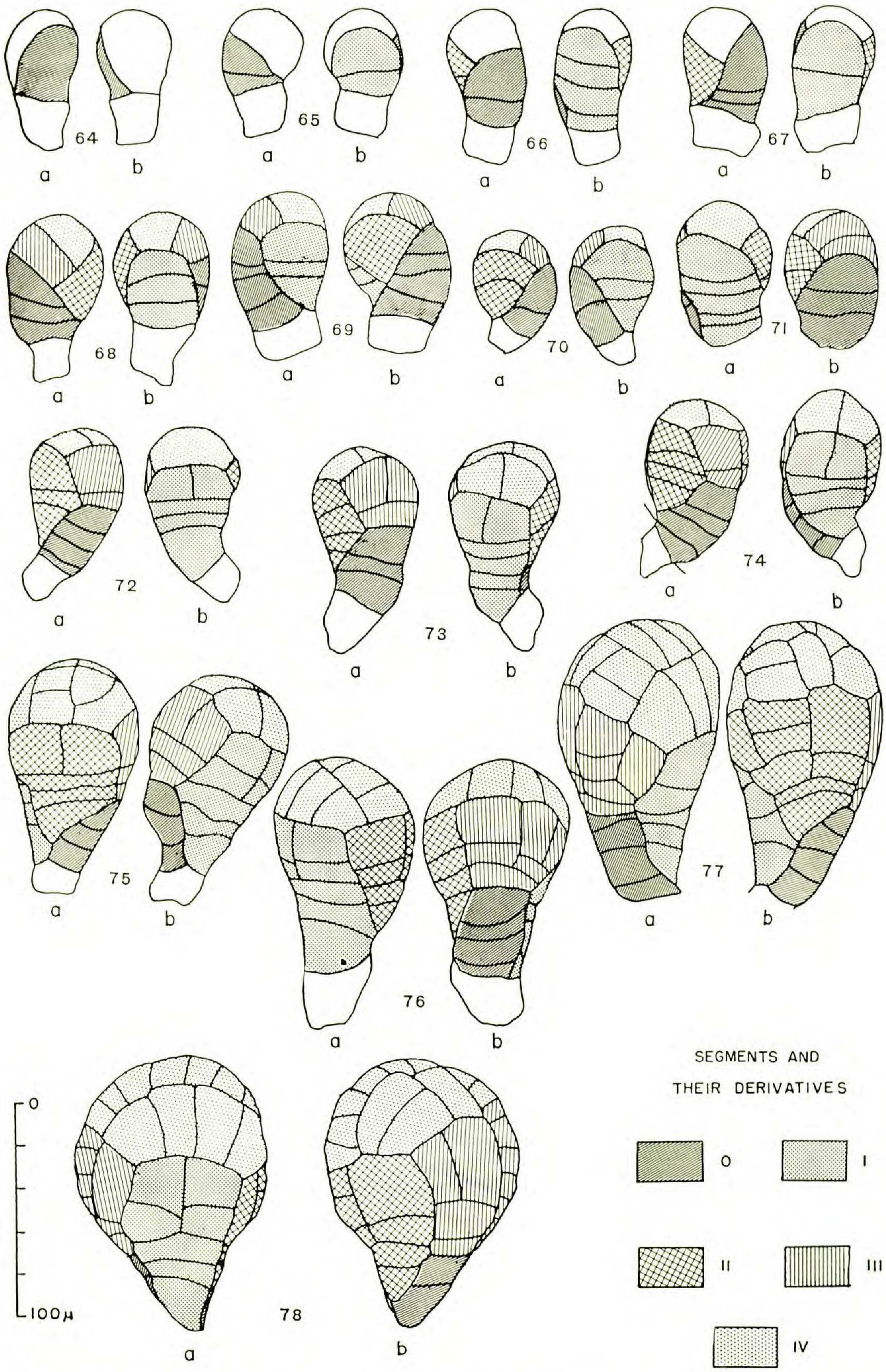
DISCUSSION

The orientation of the first division of the sporangial initial is not always the same in different species. In *Pyrrosia nuda*, as well as in *Phlebodium aureum*, the first wall formed is oblique and reaches the level of the receptacular cells. On the other hand, the first wall in *Xiphopteris serrulata* is essentially transverse and well above the cell surface of the receptacle.

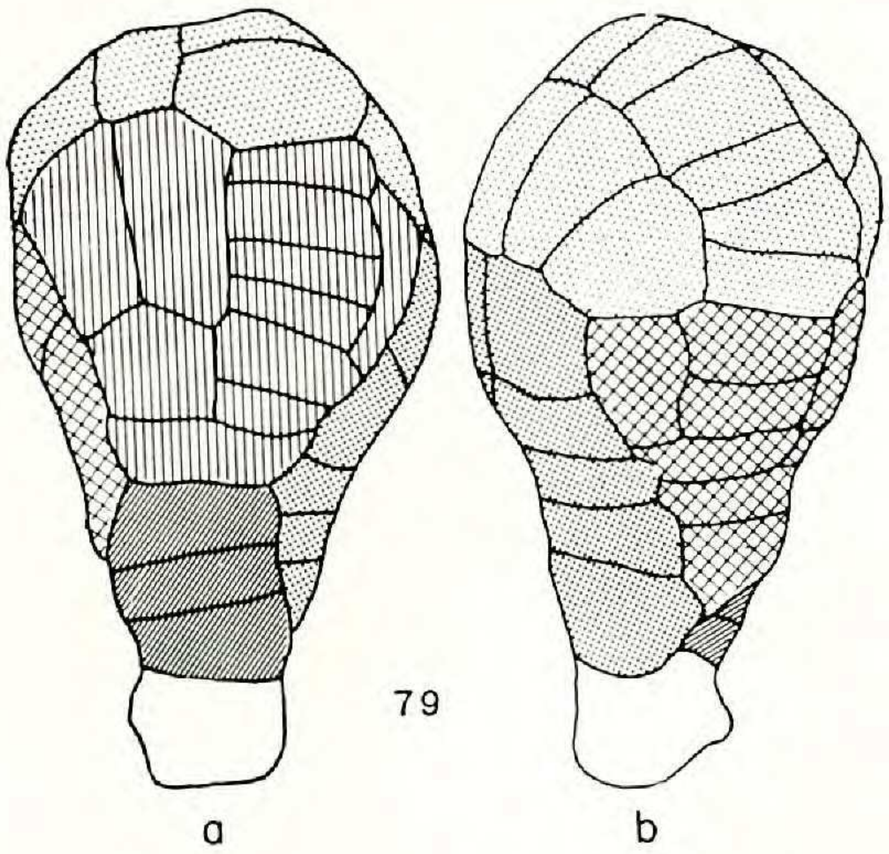
Wagner (1952) has shown the same variation in the species he examined. The first division of the sporangial initial of *Diellia* and *Asplenium* is transverse, while in *Nephrolepis* and *Davallia* it is oblique. Kündig (1888) was the first to notice the two different orientations of this cell wall. According to him, the first wall is oblique in *Asplenium* and all the other species he investigated, except *Polypodium vulgare*, where the first wall is transverse. The observations on *Asplenium* and *Polypodium* are no doubt in error, and the correct interpretation would be the reverse of that given by Kündig. As will be explained below, the structure of the mature stalk directly reflects the orientation of the first division of the sporangial initial.

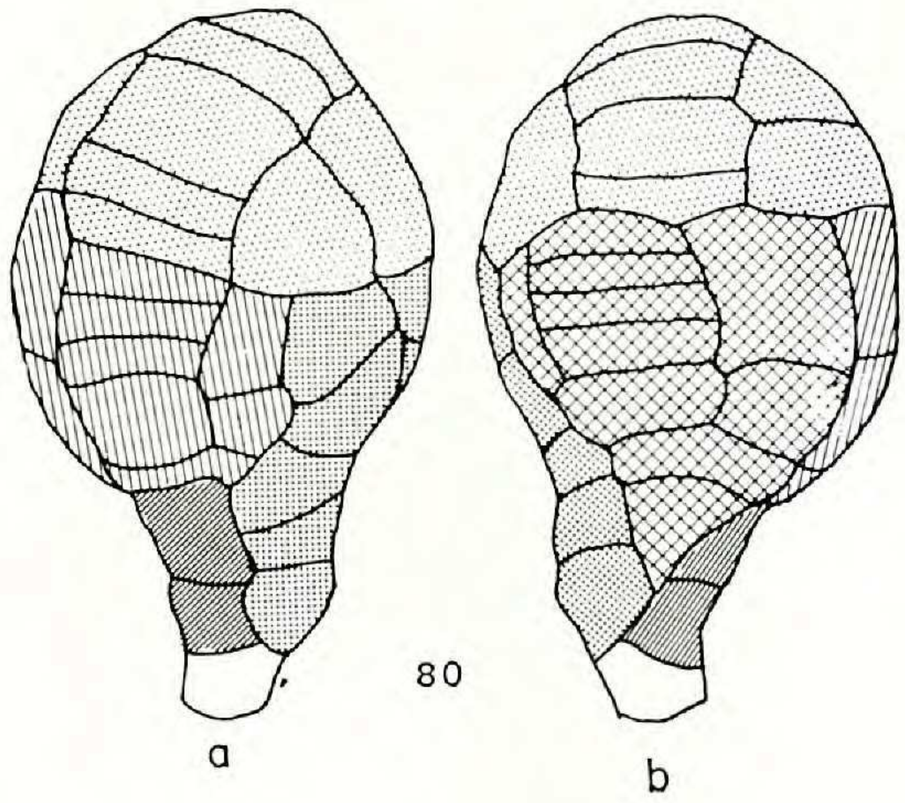
Although no division figures were seen in the stalk-forming segments of *Xiphopteris serrulata* and *Pyrrosia nuda*, there is no evidence to indicate that the walls are not intercalated to produce the sporangial stalk in these species as they are in *Phlebodium aureum*. There is certainly no indication that the stalk is produced by the activity of an apical cell.

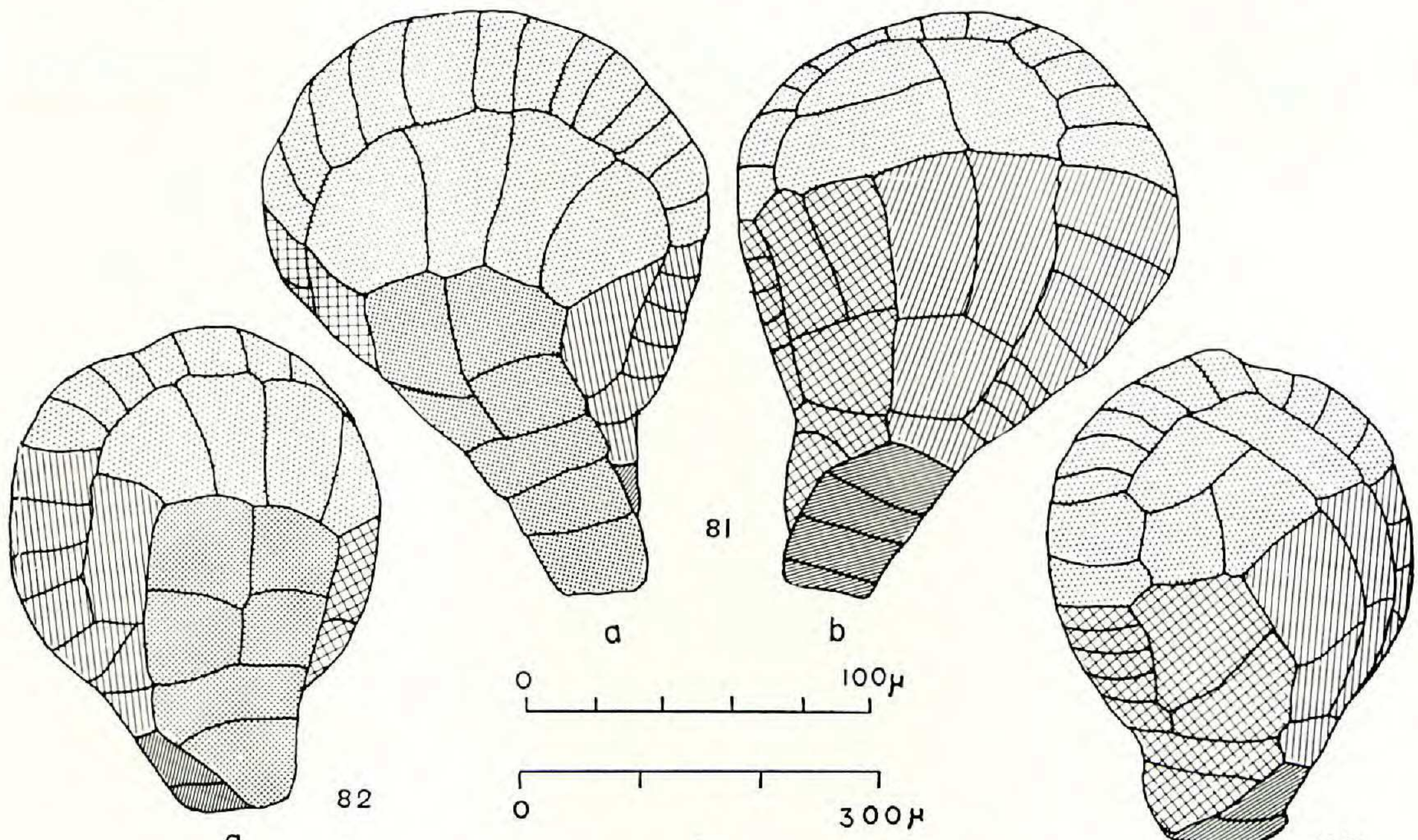
Wagner (1952) postulated that the two-rowed stalk is produced entirely by the oblique orientation of the first wall, and the one-rowed stalk results from the transverse position of this first-formed wall. The sporangial stalk of *Xiphopteris* is one-rowed and is indeed a direct result of the horizontal orientation of the first wall. All cell walls intercalated are transverse, never

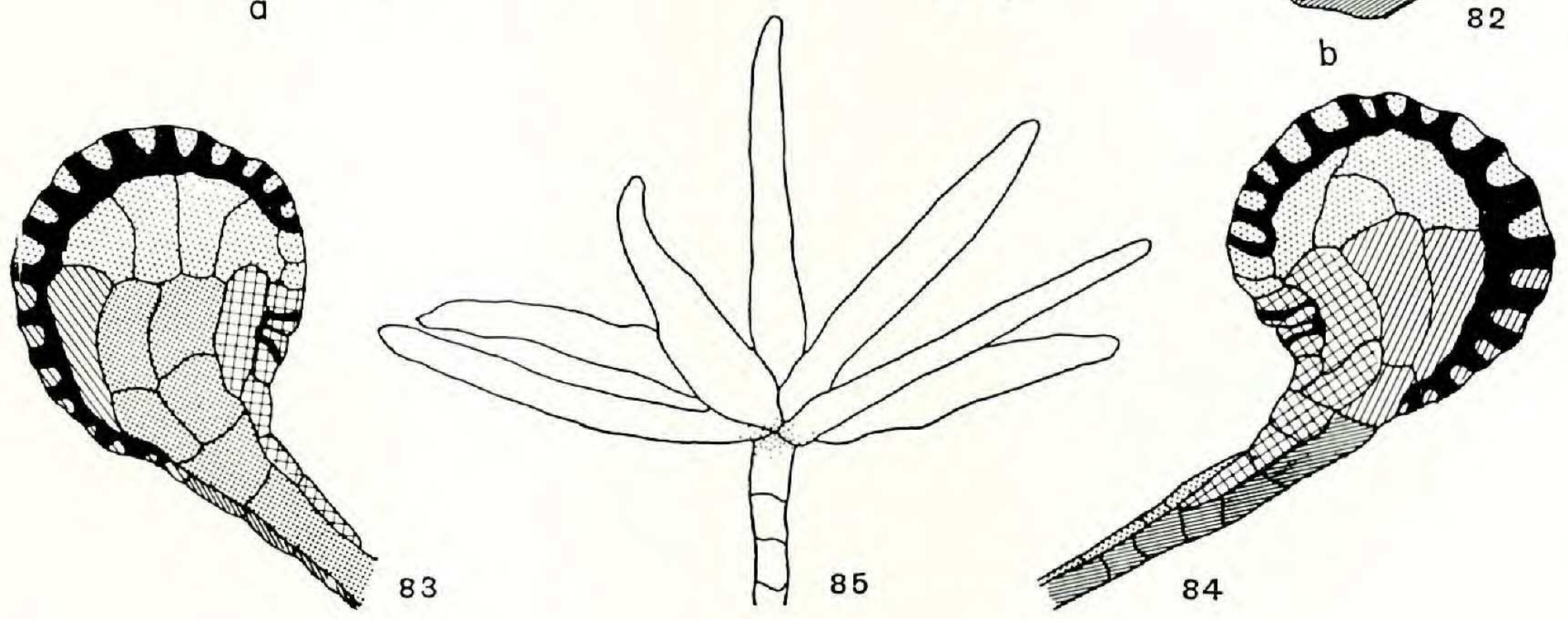


FIGS. 64–78. SPORANGIAL ONTOGENY IN *Pyrrosia nuda*: SUPERFICIAL SEGMENTATION, EARLIER STAGES.









FIGS. 79–85. SPORANGIAL ONTOGENY IN *Pyrrosia nuda*. 79–82, Superficial segmentation, later stages; 83, 84, Mature sporangium; 83, Proximal face; 84, Distal face; 85, Mature paraphysis.

longitudinal. Stalk formation in *Xiphopteris* agrees with that in *Diellia*. However, one may question Wagner's conclusion with regard to the development of the two-rowed stalk. In *Phlebodium aureum* the sporangial stalk is always two-rowed and the first division is oblique. The first wall formed in the sporangial initial of *Pyrrosia* is also oblique, but the stalk is not always two-rowed: it may be three-rowed instead. As has been pointed out in *Pyrrosia*, the two-rowed condition is not solely the result of the orientation of the first wall, but depends also on the placement of the wall which forms segment I. When segments 0 and I do not include the entire basal portion of the initial, the stalk will be three-rowed as a result of the cells contributed to it by segment II. The significance of the first wall in the structure of the stalk may then be summarized in this manner: The one-rowed stalk is produced entirely by the orientation of the first division,[2] while the two- and three-rowed stalks depend on the orientation of both the first division and that which produces segment I. The distal portion of the stalk is always three-rowed and is formed by the lower cells of segments I, II, and III.

Bower (1915) reported on the development of the sporangia of *Dipteris* and *Cheiropleuria*. The sporangial stalks of these ferns are four-rowed, and, according to him, the segmentation of the young sporangium "appears to show a regular cleavage of the segments *in two opposite rows*," and the "subdivision of the two rows of segments of the stalk by walls in the plane of the drawings has given rise to the four rows of cells of the stalk, as seen in later stages." In view of the preceding discussion which points out that there is no apical cell activity in the production of the stalk in the species examined, I suggest that a reinvestigation of the sporangia of both *Cheiropleuria* and *Dipteris* should be made, stressing stalk formation and, because of its potential morphological significance, the inner and outer segmentations of the capsule. For the present, Bower's conclusions must be accepted with reservation.

The internal divisions following the formation of segment IV are the same in *Xiphopteris serrulata*, *Pyrrosia nuda* and *Phlebodium aureum*. The four tapetal initials are produced by the mother initial in the same sequence and in the same manner as are the four capsular segments (segments I–IV). Only after the enclosed mother initial has produced the tapetal initial does it undergo a change in activity and begin to divide equally to produce the sporocytes. Moreover, as in *Phlebodium aureum*, there is no evidence to indicate that the derivatives of the tapetal initials are potentially sporogenous, nor is there any to support the view that any of the derivatives of the inner cell behave in the manner of a tapetal cell. Thus, in view of the manner in which the tapetal initials are formed, the opinion that they are better considered as inner wall cells, at least ontogenetically, is strongly supported. The central cell may be considered sporogenous only after these initials have been cut off from the mother initial.

There has been much disagreement in the application of the term "arche-

[2] A possible exception may be found in the sporangial stalk of *Dictymia*, which possesses a single cell at its base.

sporium." Kündig (1888), Müller (1893), Campbell (1905), Bower (1923), and Smith (1938) used it to refer to the central tetrahedral cell before the tapetal initials are formed. However, Kny (1895) and more recently Troll (1954) have limited its usage to the central spore-producing cell. Since the term "archesporium" is intended to refer to the first cell generation of the sporogenous tissue, it should be used only to designate the truly sporogenous initial. A more comprehensive survey of the use, or perhaps misuse, of this term was made by Bower (1908), who suggested that it be retained "merely in a descriptive sense, in those cases where the cell or cells which give rise to the sporogenous group are obvious, but in a descriptive sense only." It might be better still to avoid the use of the term and prevent confusion. This has been done by Eames (1936) and Wagner (1952), although Eames considered the central cell, prior to the formation of the tapetal initials, to represent the "primary sporogenous tissue."

Eames also reported that from the "primary sporogenous tissue" are cut off by "periclinal divisions one or two layers of thin cells which become the tapetum." I have not seen any evidence to support this statement. All of my material indicates that only one layer of tapetal initials is cut off, which, as a result of periclinal and anticlinal divisions, develops into a two-layered tapetum. It may be possible that in some ferns two series of tapetal initials are produced, but there is no evidence at present to support this statement.

The subdivision of the capsular segments is remarkably similar in *Xiphopteris*, *Pyrrosia* and *Phlebodium*. In all three, segment I contributes to a portion of the stalk and part of the proximal face of the capsule, segment II to the stomial region and the stalk, and segments III and IV to the rest of the annulus. The proximal face is formed from cells of segments I, II, III, and IV, and the distal face from those of segments II, III, and IV.

As has been pointed out by Wagner, a comparison of the "eusporangiate method" of sporangial development with the "leptosporangiate method" is highly desirable. Bower (1923) described a series showing gradual steps from the segmentation typical of eusporangiate ferns to that of leptosporangiate ferns. Similar series are also described by him for the sporangial stalk and for the capsule. His conclusions indicate that there is little fundamental difference between the two types and that the facts "appear to establish the general sequence of forms from the Eusporangiate to the Leptosporangiate, as a valid evolutionary progression."

I have shown that there has been a great deal of misunderstanding of the ontogeny of the polypodioid leptosporangium, and, in view of this, comparisons based on data of uncertain validity may be seriously questioned. A review of the literature on the development of the sporangium of the Marattiaceae and the Ophioglossaceae shows that little is known about the process and that the various authors do not agree. (For a summary of this information see Campbell, 1911, and Bower, 1923).

Before any detailed comparison can profitably be made between the two

types of development, new investigations should be made of the ontogeny of the sporangium of the eusporangiate ferns, and of the so-called "primitive" leptosporangiate ferns.

Pirard (1947) discussed the stellate paraphyses of *Niphobolus* [*Pyrrosia*] *lingua*, but these do not agree in their details with those of *Pyrrosia nuda*. The paraphyses of *P. nuda* do not have the thickenings in the cell walls of the stalk as do those of *P. lingua*, nor are the elongated cells borne on a swollen cell, but rather on one of approximately the same dimensions as the cells of the stalk. Since the various types of stellate paraphyses have been used as taxonomic characters in the genus (Giesenhagen, 1901), it is hardly surprising that those of these two species should be different.

SUMMARY

In a study of the ontogeny of the sporangia of *Xiphopteris serrulata* and *Pyrrosia nuda*, it is shown that the sporangial stalk is produced by the intercalation of cell walls in the first-formed segments of the sporangial primordium. A one-rowed stalk results directly from the horizontal orientation of the first division of the sporangial initial; two- and three-rowed stalks are produced by an oblique first division, and the number of rows depends upon the orientation of the wall forming segment I. The stalk is produced from the division products of the initial designated as segment 0 and the lowermost cells formed from segments I, II, and III. The stomial region develops in segment II, and the remainder of the annulus forms in segments III and IV. It is again suggested that the tapetal initials are better interpreted as inner wall cells of the capsule, and that the term "archesporium" be limited to designate the cell which directly gives rise to the sporocytes. Comparison of the leptosporangium with the eusporangium must be deferred until more information on both sporangial types is available. The paraphyses of *Pyrrosia nuda* are also described.

ARNOLD ARBORETUM AND GRAY HERBARIUM
HARVARD UNIVERSITY

LITERATURE CITED

BOWER, F. O. 1908. The Origin of a Land Flora. 727 pp. MacMillan, London.

———. 1915. Studies in the phylogeny of the Filicales. V. *Cheiropleuria bicuspis* (Bl.) Presl, and certain other related ferns. Ann. Bot. **29**: 495–529.

———. 1923. The Ferns. Vol. I. Analytical Examination of the Criteria of Comparison. 359 pp. University Press, Cambridge, England.

CAMPBELL, D. H. 1905. The Structure and Development of Mosses and Ferns. 657 pp. MacMillan, London.

———. 1911. The Eusporangiatae. The comparative morphology of the Ophioglossaceae and Marattiaceae. Carnegie Inst. Wash. Publ. **140.** 229 pp.

EAMES, A. J. 1936. Morphology of Vascular Plants. Lower Groups. 433 pp. McGraw-Hill, New York.

FOSTER, A. S. 1949. Practical Plant Anatomy. Ed. 2. 228 pp. D. Van Nostrand, New York.

GIESENHAGEN, K. 1901. Die Farngattung *Niphobolus*. 223 pp. Gustav Fisher, Jena.

HOLTTUM, R. E. 1954. The classification of ferns: The present position and some thoughts on future developments. Huitième Congr. Intern. Bot. Rapports & Communications, Sect. 2, 4, 5, 6: 5–8.

JOHANSEN, D. A. 1940. Plant Microtechnique. 523 pp. McGraw-Hill, New York.

KNY, L. 1895. Entwickelung von *Aspidium Filix mas* Sw. Botanische Wandtafeln mit erläuterndem Text, Abt. **9.** 411–438. Paul Parey, Berlin.

KÜNDIG, J. 1888. Beitrage zur Entwicklungsgeschichte des Polypodiaceensporangiums. Hedwigia **27:** 1–11.

MÜLLER, C. 1893. Zur Kenntniss der Entwickelungsgeschichte des Polypodiaceensporangiums. Ber. Deutsch. Bot. Ges. **11:** 54–72.

PIRARD, N. 1947. Sporanges, paraphyses, et organes connexes chez les fougères. Cellule **51:** 155–184.

SMITH, G. M. 1938. Cryptogamic Botany. Vol. II. Bryophytes and Pteridophytes. 380 pp. McGraw-Hill. New York.

TROLL, W. 1954. Allgemeine Botanik. Ein Lehrbuch auf vergleichend-biologischer Grundlage. 749 pp. F. Enke, Stuttgart.

WAGNER, W. H., JR. 1952. The fern genus *Diellia*. Its structure, affinities and taxonomy. Univ. Calif. Publ. Bot. **26:** 1–212.

WILSON, K. A. 1958. Ontogeny of the sporangium of *Phlebodium* (*Polypodium*) *aureum*. Am. Jour. Bot. **45:** 483–491.